

THE OVULE OF THE *BRUNIACEÆ*.

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INTRODUCTION.

In a recent essay by SCHÖNLAND (3) the *Bruniaceæ* are mentioned as one of the more ancient constituents of the South African Flora. The author remarks: "The *Bruniaceæ* . . . are so isolated amongst Saxifragineæ that we can also only point to their antiquity." It seemed, therefore, desirable that an investigation of the structure of the ovule and embryo-sac should be undertaken.

The family is endemic in South Africa, and out of the 12 genera 4 are represented in the Cape Peninsula, *i.e.*, *Brunia*, *Berzelia*, *Staavia*, *Audouinia*. Fortunately, these well illustrate the range of types met with in the order, and it is very unlikely that any other genus would differ widely from these four. One species of each genus has been investigated, and the structure has been found to be very constant throughout. The primary object of the research was the investigation of the structure of the mature ovule, but it was necessary to study certain phases of development in order to explain the mature structure, and these are therefore included in the present account. The methods used have been those usually employed in cytological work, the fixing agents used having been (i.) chromacetic acid—1·5 grams chromic oxide, 7 c.c. acetic acid, 250 c.c. water; (ii.) picric, acetic, corrosive sublimate solution. The latter was found the most satisfactory.

An exceedingly accurate account of the position and external characters of the ovule in the genera investigated is given by BENTHAM and HOOKER (1). In *Berzelia* the ovary is unilocular and there is only a single pendulous, anatropous ovule. In *Staavia* and *Brunia* the ovary is bilocular, in the former genus with one ovule in each loculus, in *Brunia nodiflora* with two. In *Audouinia* the ovary is trilocular with two ovules

in each loculus. In all cases the ovary is inferior or half inferior, and the ovules are pendulous and anatropous with a dorsal raphe. The foregoing description, while based on a study of the plants, is merely a repetition of that given by BENTHAM and HOOKER (*loc. cit.*), and is inserted as an introduction to the study of the ovule.

DESCRIPTION.

In each of the four genera mentioned the young ovule (at about the time of megasporogenesis) consists of a small nucellus with rather large cells and a single massive integument with somewhat smaller cells and a very long and slender micropyle. The contents of the nucellus cells are scanty, but those of the cells of the integument fairly dense (Fig. 2). It may be mentioned that in earlier stages, when the rudimentary integument first appears, there is never any indication of two integuments which subsequently fuse. If, therefore, the single integument really represents two integuments fused, it is necessary to assume that congenital fusion has occurred. In the writer's opinion such an assumption would require strong evidence to support it, which, in the present instance, is not the case. The order is (as pointed out above) so isolated, and its relationship so obscure that even a comparison with the ovule in other orders of the *Rosales* in this respect would scarcely be profitable.

The megaspore mother cell becomes much longer than its neighbours, and is separated from the apex of the nucellus by about two cells.

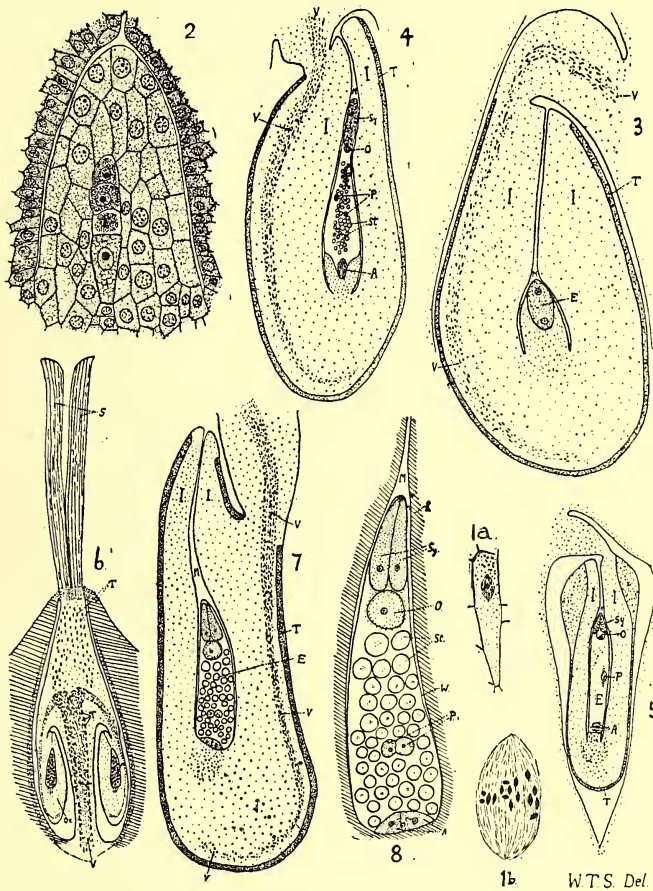
The heterotypic division has been seen, but owing to the very small size of the nuclei it was difficult to be certain of the number of chromosomes. Figs. 1*a* and 1*b* show respectively the general appearance of the mother cell, and the chromosomes of the heterotypic division, of which there appear to be 16 (*i.e.*, 8 to each daughter nucleus). In sporophytic divisions it has been quite impossible to attempt a count of chromosomes.

The divisions of the mother cell result in the usual row of four megaspores, of which the lowest becomes the embryo sac (Fig. 2). Attention was paid to this point as it is not uncommon in the *Rosales* (at least, in *Leguminosæ* and *Rosaceæ*) for one of the other megaspores to be functional. A case of this kind was recorded by the writer in *Cassia* (2)*. Such cases are, however, very exceptional, and while the presence of so pronounced a peculiarity would have undoubtedly indicated a close relationship to other *Rosales*, its absence cannot be regarded as evidence to the contrary.

The young embryo sac very rapidly grows upwards, absorbing the cells above it, and before the second nuclear division in the sac it has reached the apex of the nucellus (Fig. 3).

* References to other cases will be found in the paper cited.

Unfortunately, no later stage than this was obtained in *Audouinia*, but there is every indication that the mature structure would be similar to the other three genera. In these the further development results in the more or less complete absorption of the nucellus. The amount of nucellar tissue which remains in the mature ovule at the base of the embryo-sac



seems to vary inversely with the number of ovules in the ovary. In *Berzelia* (one ovule) a considerable proportion of the base of the nucellus remains (Fig. 4), in *Staavia* (2 ovules) a very small part remains (Fig. 5), whereas in *Brunia* (4 ovules) the whole of the nucellus disappears (Figs. 6, 7, 8).

The nuclear structure of the mature sac is perfectly normal: 2 pyriform synergids, a spherical egg cell, 2 polar nuclei, fusing before

fertilisation, and 3 antipodals which are not persistent. The most striking feature of the embryo-sac in *Brunia* is that it is completely filled with large starch grains (Figs. 6-8). I know of no other instance where an embryo-sac is packed with starch grains as it is in this plant. Starch grains are present also in *Berzelia*, but much smaller and not filling the sac (Fig. 4). They are apparently absent from the embryo-sac of *Staavia* (Fig. 5).*

SUMMARY AND CONCLUSIONS.

The main points of the above account may be briefly summarised as follows:—

The ovule of the *Bruniaceæ* is pendulous and anatropous, with a dorsal raphe. There is a single massive integument with a long slender micropyle. In *Brunia* the embryo-sac is packed with starch and is all that remains of the nucellus. In *Berzelia* and *Staavia* a little of the basal nucellar tissue persists.

In development the megaspore mother cell is about the third cell from the apex of the small nucellus. The usual row of four megaspores develops, of which the lowest becomes functional.

The developing embryo-sac very soon absorbs the tissues above it, and so reaches the apex of the nucellus.

The only conclusion to be drawn from this study is the same to which SCHÖNLAND (*loc. cit.*) was led—namely that the *Bruniaceæ* are very isolated in the cohort to which they are usually attached. Whether the characters of the ovule also point to its antiquity may perhaps be questioned. The single integument might be regarded as a primitive character, if it were not associated with the ovule of the *Compositæ*, while in some of those orders generally regarded as primitive (*e.g.*, *Proteaceæ*) two integuments are found. Possibly the word “antiquity” was not used by SCHÖNLAND in a philogenetic sense, but antiquity in the South African Flora must (if we accept the author’s conclusions), imply also phylogenetic antiquity.

The other characters of the ovule rather tend to agree with essentially modern types (*e.g.*, *Compositæ*), than with primitive (*e.g.*, *Ranunculaceæ*).

In conclusion, I am glad to take this opportunity of thanking Mr. E. P. Phillips, who accompanied me on a collecting trip, and whose intimate acquaintance with the local flora was of great assistance in obtaining the requisite material for this study.

* Since the above was written, Miss E. L. Stephens has kindly shown me some slides of the embryo-sac of *Brunia*, in which she has demonstrated that the starch almost completely disappears before fertilisation. She has also drawn my attention to a paper by D’Hubert (D’Hubert, E., *Recherches sur le sac embryonnaire des plantes grasses*, Ann. Sci. Nat. Bot., viii. 2: 37-128, pls. 1-3, fig. 66, 1896), in which a similar formation and subsequent absorption of starch is noted in various fleshy plants.

LITERATURE CITED.

Citations of papers not available to the writer have purposely been omitted. The more important are given in COULTER and CHAMBERLAIN'S "Morphology of Angiosperms," 1903.

1. BENTHAM, G., and HOOKER, J. D., "*Genera plantarum.*" London. 1842.
2. SAXTON, W. T., "On the Development of the Ovule and Embryo-sac in *Cassia tomentosa*, Lamk." *Trans. S. A. Phil. Soc.*, **18**: 1-5, pls. 1, 2, 1907.
3. SCHÖNLAND, S., "A Study of some Facts and Theories bearing upon the Question of the Origin of the Angiospermous Flora of South Africa." *Trans. S. A. Phil. Soc.*, **18**: 321-367. 1907.

EXPLANATION OF FIGURES.

Sections were cut with a rocking microtome, and drawings made with a Zeiss microscope, lenses, and camera lucida. Except Figs. 1 and 2 the drawings are made from more than one section of a series. They are, however, accurately drawn to scale. In all: A = Antipodals. E = Embryo-sac. I = Integument. M = Micropyle. O = Oosphere. Ov = Ovule. P = Polar nuclei. S = Style. St = Starch grains. Sy = Synergids. T = Tannin (?) containing cells. V = Vascular bundle.

FIG.

- 1a. Megaspore mother cell dividing *Staavia glutinosa*, Thunb. $\times 270$.
- 1b. Spindle of Fig. 1a. $\times 1000$.
2. Row of 4 megaspores in nucellus and a few cells of the integument. *Audouinia capitata*, Brongn. $\times 360$.
3. Ovule with bi-nucleate embryo-sac. *Audouinia capitata*, Brongn. $\times 90$.
4. Mature ovule of *Berzelia languinosa*, Brongn. $\times 75$.
5. Mature ovule of *Staavia glutinosa*, Thunb. $\times 40$.
6. Diagrammatic longitudinal section of the ovary of *Brunia nodiflora*, Linn. $\times 17$.
7. Mature ovule of *Brunia nodiflora*, Linn. $\times 75$.
8. Embryo-sac of *Brunia nodiflora*, Linn. $\times 155$.